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ORIGINAL ARTICLE

Effects of crown length on indole acetic acid (IAA) amounts in cambial region tissues in lower and upper trunks of sugi cultivars (*Cryptomeria japonica*) in September

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Abstract Indole acetic acid (IAA) was believed to be an important regulator in xylem formation in conifers. However, few studies have been done on the endogenous amount of IAA in cambial region tissues in sugi (*Cryptomeria japonica*) trees. In this study, we report the IAA amounts in the lower and upper trunk of mature sugi cultivars (Kumotoshi, Yaichi and Obiaka) in September, and the effects of growth traits on the IAA amounts. The effect of height position (lower or upper trunk) on IAA amounts was found to be larger than that of genetic variation (Kumotoshi, Yaichi or Obiaka) by two-way ANOVA. There was no significant interaction effect (genetic variation × height position). The IAA amounts of all trees varied from 3 to 42 ng/cm^2 at the lower trunk and 9 to 47 ng/cm^2 at the upper trunk. Crown length and distance from crown base had significant positive and negative effects on IAA amounts in the trunk of sugi cultivars, respectively. Distance from crown base had a larger effect on IAA amounts than crown length. In Yaichi, taller trees had larger IAA amounts at both the lower and upper trunk.

Keywords Sugi · IAA · Crown length · Distance from the crown base

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Introduction

Softwood is one of the most important renewable resources in the world, and is mainly used in the structural components of wooden structures. Many studies of wood formation in economically important conifers have been done because wood formation affects the quality and quantity of the wood produced [1–5]. These studies have focused on the role of plant growth regulators, especially indole acetic acid (IAA), in wood formation. In *Abies balsamea*, it was reported that the defoliation of current-year shoots inhibited tracheid production and decreased the IAA contents, while exogenous IAA compensated for the effect of defoliation in the stem [6]. In *Pinus contorta* and *Pinus densiflora*, the IAA amounts in the cambial region tissues varied seasonally, being higher in summer and lower in autumn and winter [7, 8]. In *Pinus sylvestris*, the application of exogenous IAA to disbudded segments increased the number of lignified tracheids in a dose-dependent manner [9]. Therefore, it was assumed that IAA was actively synthesized in elongating shoot apices and was transported to the stem cambium, where it then stimulated tracheid production. In *Pinus resinosa*, it was hypothesized that the earlywood to latewood transition was induced by a decrease in IAA contents in the cambial region tissues from early to late in the season [10]. On the other hand, it was suggested that the tracheid productions was not directly related to the IAA concentration in the cambium of pine trees [11]. However, this study did not examine the effects of IAA amounts on tracheid differentiation (cell diameter, cell wall thickness, microfibril angle of S_2 layer). Based on the radial distribution pattern of the IAA amounts from the phloem to the developed xylem in *P. sylvestris*, IAA was assumed to control xylem differentiation as a "morfogen" [12]. Based on these studies, IAA was believed to be an important

regulator in xylem formation in conifers. In these studies, many of the experiments involving the application of exogenous IAA were limited to younger cambium, and it was reported that there were no clear effects on the production of tracheids in the older cambium of defoliated stem segments [13]. It was pointed out that application experiments sometimes show conflicting results and should be viewed with caution [14]. In application experiments, the observed response in cambium may be induced by unphysiological IAA levels, or resulting internal IAA levels by application may be different from the expected IAA levels from the applied exogenous IAA amounts. Therefore, it is very important to understand the variation of endogenous IAA contents in the mature cambial region tissues to elucidate the process of wood formation in conifers. However, the contents of endogenous IAA in cambial region tissues were examined in limited species, and there have not been enough studies on these endogenous IAA contents to elucidate the role of IAA in xylem formation.

Sugi (*Cryptomeria japonica*, Japanese cedar) is one of the important plantation species in Japan. This domestic wood is mainly used for structural applications. This domestic tree shows inter- and intra-tree variations in wood properties [15]. Therefore, studies of the endogenous IAA contents in this domestic tree should be done precisely to elucidate the role of IAA in xylem formation and the effect on variations in wood properties. However, few studies have been done on the endogenous IAA amounts in cambial region tissues in sugi trees [16]. In Kyushu, Japan, many sugi cultivars are planted for wood production, and growth traits vary among sugi cultivars. These domestic trees are usually planted at a density of 3000 trees/ha. Competition between trees begins as trees grow larger, and then the lower branches of sugi tees naturally wither and fall. The characteristics of sugi cultivars in growth traits may affect the crown size. In *P. densiflora* and *P. sylvestris*, it was reported that differences in crown size (induced by pruning) affected the IAA amounts in the cambial regions of trees at different stem heights [8, 11, 17]. The height position in the trunk affected the IAA amount in the cambial region tissues of pine trees, because IAA synthesized at the crown was transported to the cambium in the trunk [7, 8]. Therefore, in sugi cultivars, the differences in crown size and the height position in the trunk may affect the IAA amounts in the cambial regions of the stem. In addition, the IAA amounts in sugi cultivars may vary seasonally as previously reported in pine trees [7, 8], and data regarding the seasonal variation of IAA amounts may be important for intra-ring variation of wood properties. In this study, however, we focused on inter-tree variation of the IAA amounts, and these data may be important for inter-tree variation of wood properties. As a first step study on the IAA amounts in sugi trees, we tried to clarify possible indexes that might affect IAA amounts in cambial region tissues in one season (IAA amounts in September). Latewood formation is assumed to be done in September in sugi trees grown at southern Kyushu, Japan, and latewood contributes much more than earlywood to the mechanical properties of softwood. Therefore, we examined the IAA amounts in the trunk of sugi cultivars with different growth traits in September.

The objectives of the current study were to examine: (1) the absolute value of the IAA amounts in the cambial region tissues at the lower and upper trunk; (2) the effects of growth traits on the IAA amounts in the cambial region tissues at the lower and upper trunk in sugi cultivars in September.

Materials and methods

Sample trees and samples for IAA quantification

The sugi cultivars (Kumotoshi, Yaichi and Obiaka) shown in Table 1 were used. The sugi cultivars were 41 years old. These trees had been planted in a sugi cultivar experimental stand (initial densities 4000 trees/ha) established in the experimental forest of Miyazaki University. Thinning had been carried out at the sugi cultivar stands. As shown in Table 1, 29 sugi trees with different growth traits were selected randomly as sample trees. The average annual temperature and precipitation at the experimental forest at Miyazaki University from 2001 to 2011 were 17.3 °C and 2793 mm, respectively. The altitude of the stands used in the current study ranged from 100 to 350 m.

For the measurement of the IAA amounts in cambial region tissues, samples [3 (T) × 5 (L) × 1 cm (R)] of cambial region tissues sandwiched by the outer bark and the outermost wood were obtained from the sample trees listed in Table 1. The samples were obtained from a point 7.0 m above the ground (upper trunk) and from a point 1.2 m above the ground (lower trunk) in three sugi cultivars in September 2008 (2 positions × 9 or 11 trees × 3 cultivars, for a total of 58 samples). Samples were stored immediately after the sample collection and stored in liquid nitrogen before extraction.

Measurements of indexes for evaluating growth traits

As indexes for evaluating growth traits, we used tree height (H), diameter at breast height (DBH), crown length (CL), crown width (CW), crown length ratio (crown length-to-tree height ratio, CL ratio), crown surface area (CSA) and crown volume (CV). The diameter at breast height (DBH) and the tree height were measured with a tape measure and ultrasonic hypsometer (Vertex III, Haglof, Inc.),

Table 1 Growth parameters of sample trees

Cultivar	Age	*n*	DBH (cm)	H (m)	CL (m)	CW (m)	CSA (m^2)	CV (m^3)	CL ratio (%)
Kumotoshi	41	9	20.4 (2.5)	18.7 (1.8)	8.0 (1.1)	2.84 (0.66)	36.3 (11.7)	18.2 (9.0)	44.0 (6.1)
Yaichi	41	11	24.8 (5.1)	21.0 (2.3)	8.1 (2.4)	2.85 (0.76)	37.7 (18.4)	19.7 (12.9)	38.1 (4.0)
Obiaka	41	9	21.9 (3.7)	18.2 (1.5)	6.9 (0.8)	2.35 (0.40)	25.7 (7.2)	10.5 (5.0)	37.8 (8.0)

The value of DBH, H, CL, CW, CSA, CV and CL ratio represents the average value of sample trees, and the values in parentheses represent the standard deviations. *n* number of sample trees, *DBH* diameter at breast height, *H* tree height, *CL* crown length, *CW* crown width, *CSA* crown surface area, *CV* crown volume, *CL ratio* crown length-to-tree height ratio

respectively. The height of crown base was measured with ultrasonic hypsometer (Vertex III, Haglof, Inc.). The crown length was calculated from the height of crown base and tree height. The widths at the crown base parallel and right to the slope of the stand were measured with a tape measure. The crown width was averaged the widths of two directions. We calculated the crown surface and the crown volume from the crown width and crown length, considering the form of the crown as a cone [18].

Measurements of IAA amounts in cambial region tissues

IAA in cambial region tissues was identified and quantified by liquid chromatography/mass spectrometry (LC/MS/MS). Samples were homogenized and extracted in 1 h by methanol with antioxidant medium (0.02 M diethyldithiocarbamic acid, Wako, Ltd.). Methanol extraction was repeated three times at 4 °C in darkness. For the quantification of IAA amounts, 1 µg of deuterium IAA (Sigma Co., Ltd, D_2-IAA, 97 % contents) was added to the methanol for extraction as an internal standard. The extracts were evaporated and the residues were dissolved in 10-ml distilled water, and then the aqueous solutions were adjusted to pH 2.5 by formic acid. The supernatants were obtained from the aqueous solutions by centrifugal separation, loaded onto reverse-phase cartridges (sep-pack cartridge, C18 500 mg, Waters), and eluted with 1 ml 80 % methanol adjusted to pH 2.5. The effluents were subjected to LC/MS/MS.

LC/MS/MS analysis was carried out using a liquid chromatograph (2695, Waters) coupled to a quadrupole mass spectrometer (Q-micro, Waters) with an ion source operated in the ESI mode. The column was a TSKgel ODS-100 V (100 × 2.0 mm, TOSOH), and the flow rate was 0.2 ml/min. As the mobile phase, 45 % methanol containing 0.5 % acetic acid was used. The mass spectrometer was run in positive ion mode and multiple reaction monitoring (MRM) mode. For the identification of endogenous IAA, the retention time on the liquid chromatograph and the parent ion (m/z 176 (M^+)) and fragment ions (m/z 76.9, 103, 130) of authentic IAA (Merck, 99 % contents) was used. For the quantification of endogenous IAA, the sensitivity of LC/MS/MS was tuned using authentic IAA, and a calibration curve was obtained from an analysis of samples of D_2-IAA and authentic IAA with different mixing ratios. From the MRM chromatogram of endogenous IAA (parent ion: m/z 176, fragment ion: m/z 130) and D_2-IAA (parent ion: m/z 178, fragment ion: m/z 132) (Fig. 1), the peak area ratio (area of endogenous IAA/area of D_2-IAA) was obtained, and then the IAA amounts of the samples were calculated using the calibration curve from the obtained peak area ratio. The proportion of developing xylem included in samples depends on the activity of cambium, and tissues (phloem, cambium and developing xylem) differ widely in their concentrations of IAA [12]. Therefore, the IAA amount (ng) per sample weight (g) was affected by the increase in sample weight during xylem formation [14]. In the current study, the IAA amount of the cambial region tissues was shown in the IAA amount (ng) per cambium area (L × T cm^2) (ng/cm^2).

Statistical analysis

For statistical analysis of the obtained data, statistical analysis software (SPSS ver. 16 with Regression and Advanced Models) was used. By two-way ANOVA and multiple comparisons tests (Tukey's HSD test and Bonferroni test), the significant differences of the IAA amounts between trees and height positions were examined. By one-way ANOVA and multiple comparisons tests (Tukey's HSD test and Bonferroni test), the significant differences of the growth traits among sugi cultivars were examined. When equality of the variances of the data was not recognized, a non-parametric test (Kruskal–Wallis test) and multiple comparisons tests (Tamhane test and Dunnet T3 test) were used. By multiple linear regression analysis, predictor equation of IAA amounts was determined.

Results

IAA amounts at lower and upper trunks of sugi cultivars

As shown in Fig. 2, in cambial region tissues of all sugi cultivars except a tree with very narrow annual ring per

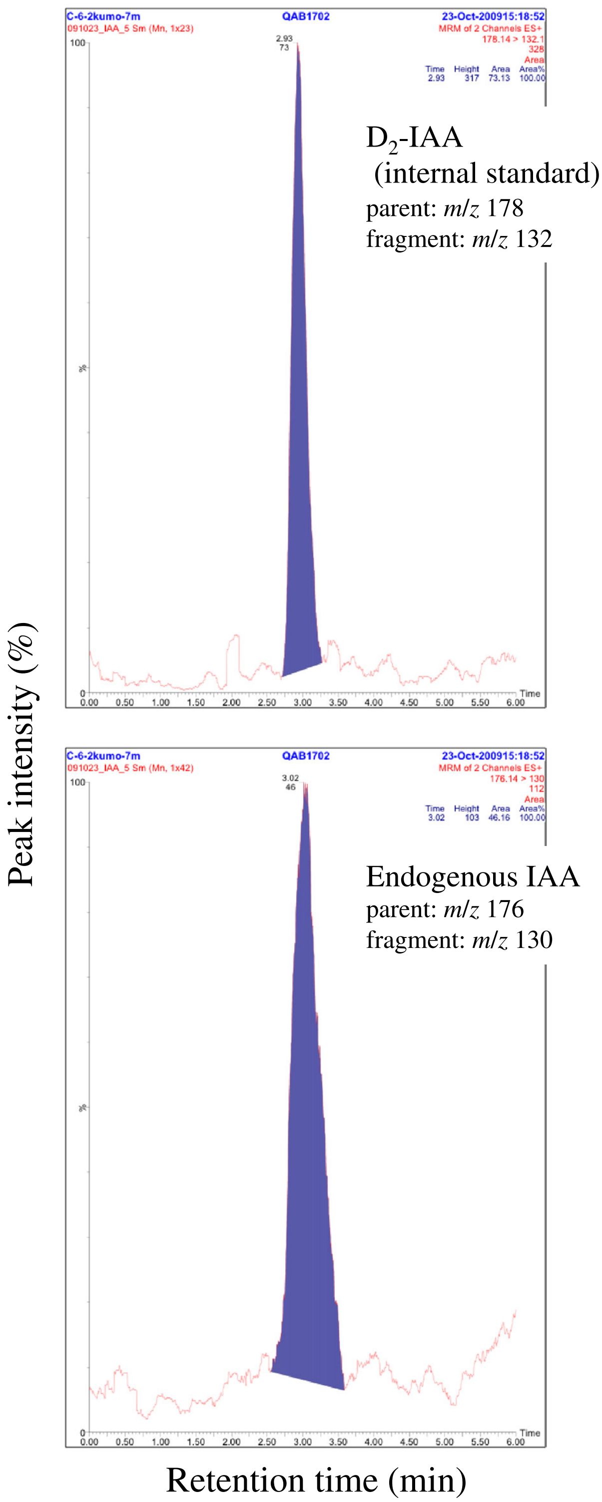

Fig. 1 MRM chromatogram of endogenous IAA and D_2-IAA (internal standard). *MRM* multiple reaction monitoring

each cultivar, latewood formation was observed in September. The IAA amounts in cambial region tissues in September at the lower and upper trunks of sugi cultivars are shown in Fig. 3. As shown in Fig. 3, Kumotoshi had the highest average IAA amount at both the lower and upper trunks. In sugi cultivars, the average IAA amounts at the upper trunk were greater than those at the lower trunk. By two-way ANOVA, it was recognized that there was a significant difference between the IAA amounts at the lower and upper trunks ($p < 0.01$), although there was no significant difference among the IAA amounts of Kumotoshi, Yaichi, Obiaka ($p = 0.09$). Also, the interaction effect (genetic variation × height position) was small ($p = 0.81$). The IAA amounts of all trees at the lower and upper trunks ranged from 3 to 42 ng/cm^2 and 9 to 47 ng/cm^2, respectively. The sampling positions were 1.2 and 7.0 m above ground. These two types of samples were different in the distance from crown base. In addition, the distance from crown base to sampling position in both upper and lower trunk varied among trees, because height of crown base varied among trees. In all samples (upper and lower trunk), there was a negative significant correlation between distance from crown base to sampling position and the IAA amount in the trunk (Fig. 4, $p < 0.01$). Form these results, it was demonstrated that the effect of genetic variations on IAA amounts was small and IAA amounts in the trunk decreased with the distance from crown base in sugi cultivars.

Growth traits of sugi cultivars

The growth traits of each sugi cultivar were shown in Table 1. Tree height was significantly different among sugi cultivars [non-parametric test (Kruskal–Wallis test), $p < 0.05$]. Yaichi trees were significantly taller than Kumotoshi and Obiaka [multiple comparisons (Tamhane test and Dunnett T3 test), $p < 0.05$ and $p < 0.01$, respectively]. Therefore, height of crown base and distance from sampling position from crown base of Yaichi trees (data not shown) were also significantly larger than other cultivars [multiple comparisons (Tamhane test and Dunnett T3 test), $p < 0.05$]. Obiaka had smaller crown length, crown width, crown surface area, crown volume and crown length ratio than other sugi cultivars (Table 1). However, there was no significant difference of these indexes among sugi cultivars.

Effects of growth traits on the variation of IAA amounts in sugi cultivars

As shown in Table 2, correlation coefficients (Pearson correlation coefficients) between growth indexes and IAA amounts were examined. It was recognized that crown length had larger positive effects on IAA amounts in lower and upper trunk than other growth indexes. In Yaichi, the correlation coefficient between crown length and IAA

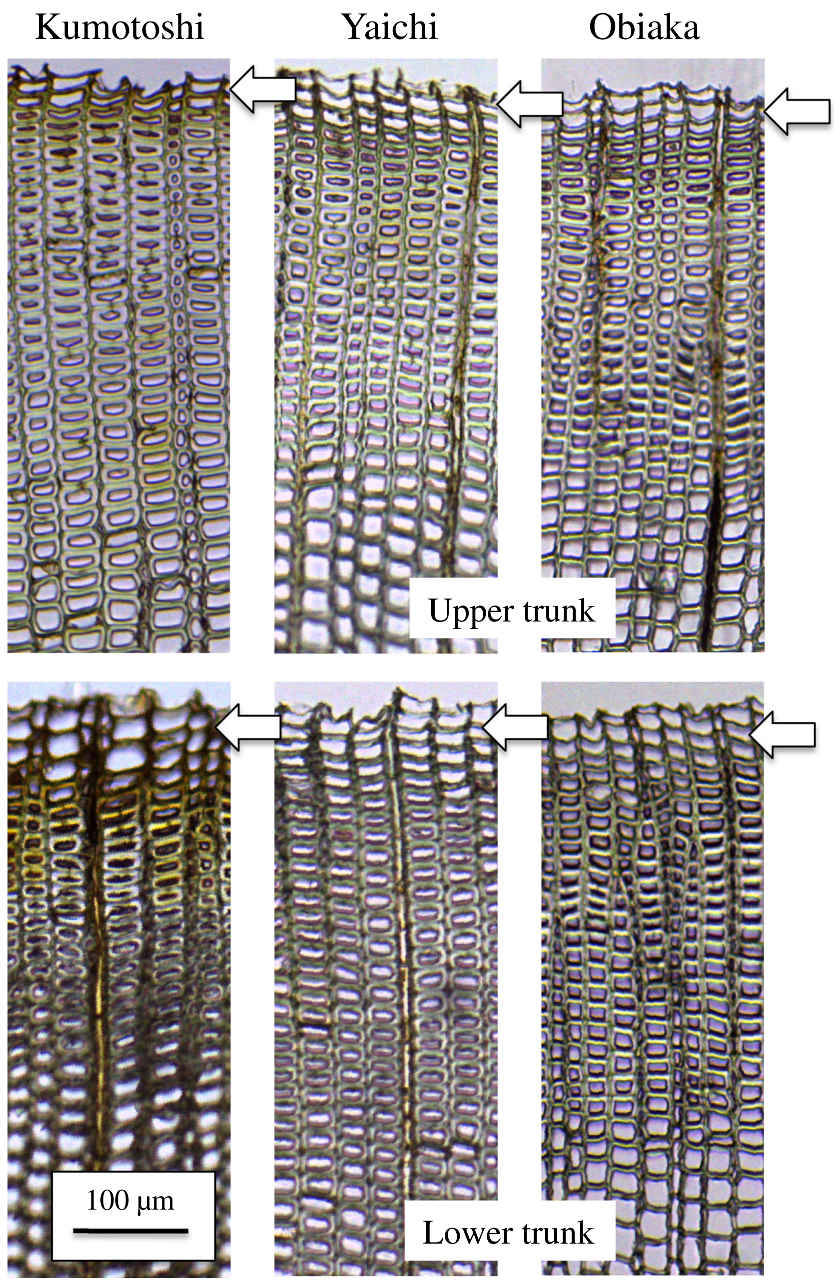

Fig. 2 Latewood formation at sampling date (September) of sugi cultivars. The cross sections were obtained from samples for IAA measurements. The cambial region tissues without secondary wall were removed and homogenized for methanol extraction. Latewood tracheids in secondary wall formation were observed (*arrows*)

amounts was larger than those in other cultivars (Fig. 5). As shown in Fig. 6, in Yaichi, tree height had a positive significant effect on the IAA amounts at both the lower and upper trunks ($p < 0.05$, $p < 0.01$, respectively). However, in Kumotoshi and Obiaka, there was no significant correlation between tree height and the IAA amount in the trunk. As shown in Fig. 7, there was a significant positive correlation between tree height and crown length in Yaichi ($p < 0.01$), although there was no significant correlation in Kumotoshi and Obiaka. Therefore, it was assumed that in Yaichi, taller trees had larger IAA amounts in cambial region tissues, because taller trees had larger crown sizes.

From current study, it was assumed that crown length (CL) and distance from the crown base (DCB) were effective parameters for predictions of IAA amounts. By multiple linear regression analysis, predictor equation was determined as follows:

$$\text{IAA amounts} = 13.2 + 2.12 \times \text{CL} - 1.23 \times \text{DCB}$$

Although this equation can help prediction of the variation of IAA amounts ($p < 0.001$), this equation cannot explain the variation of IAA amounts sufficiently ($R^2 = 0.246$). Based on the standardized partial regression coefficients (CL 0.304, DCB −0.374), it was recognized

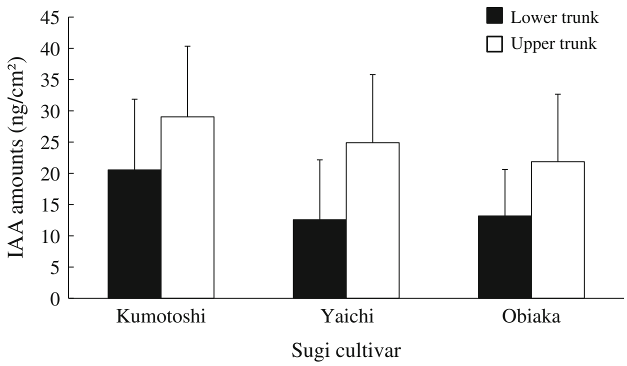

Fig. 3 IAA amounts in cambial region tissues of sugi cultivars. There was a significant difference in the IAA amounts between the *lower trunk* and *upper trunk* ($p < 0.01$). *Lower trunk* a point 1.2 m above the ground, *upper trunk* a point 7.0 m above the ground (sugi cultivars)

that the distance from the crown base had a larger effect on IAA amounts in the trunk of these sugi cultivars than that of crown length.

Discussion

Latewood formation was observed in our almost sample trees in September. However, in sugi trees (20 years old, grown in Tokyo, Japan), cessation of cell production in many trees was recognized in September or earlier season [16]. The average annual temperature in our test stand was higher than that in the test stand in Tokyo, Japan. The difference of environmental factor may affect the cessation season of xylem formation in trees [19]. It was reported that the IAA amounts of cambial region tissues in the trunks of *P. densiflora* (20 years old, September), *P. sylvestris* (20 years old, May to August) and *P. sylvestris* (43 years old, July) ranged from 50 to 200 ng/cm^2 [17], from 40 to 120 ng/cm^2 [14], and from 33 to 168 ng/cm^2 [12], respectively. The IAA amounts of sugi trees in September (Fig. 3) were assumed to be smaller than those previously reported in pine trees.

In *P. contorta* (20 years old, 5 m in height, 10–15 cm in diameter at 1.7 m above the ground), the IAA levels in cambial region tissues were highest in the trunk near the crown base from March to November [7]. And it was concluded that an increasing IAA concentration gradient was present from shoot apex toward crown base, and a decreasing gradient present from crown base to soil level. Therefore, in *P. contorta*, position in the crown and distance from the crown affected the IAA amounts in cambial region tissues in the trunk. In *P. densiflora* (20 years old), cambial region tissues at the upper trunks of trees with larger CL ratios showed greater IAA amounts than those at the lower trunks of trees with smaller CL ratios [8]. The CL rations of sample trees were reduced to 60, 40 and 20 % by pruning. In *P. sylvestris* (50 years old), the cambial region tissues of trees with a large crown and fast growth rate (F-trees) showed greater IAA amounts than those of trees with a small crown and slow growth rate [11]. And it was also reported that pruning F-trees (reduced the needle biomass by about 70 %) decreased the IAA amounts in cambial region tissues. In these pine trees, the crown size affected the IAA amounts in cambial region tissues in the trunk. In sugi trees (20 years old), auxin levels in cambial region tissues of trees with different crown length ratios (60, 40 and 20 % by pruning) were examined by avena straight-growth test [16]. In this study on pruning sugi trees, it was reported that auxin levels in trees with smaller crown length ratios decreased rapidly. In our study on intact sugi

Fig. 4 Effects of distance from crown base on IAA amounts in cambial region tissues. There was a negative correlation between distance from crown base and IAA amounts at all samples. $^{**}p < 0.01$

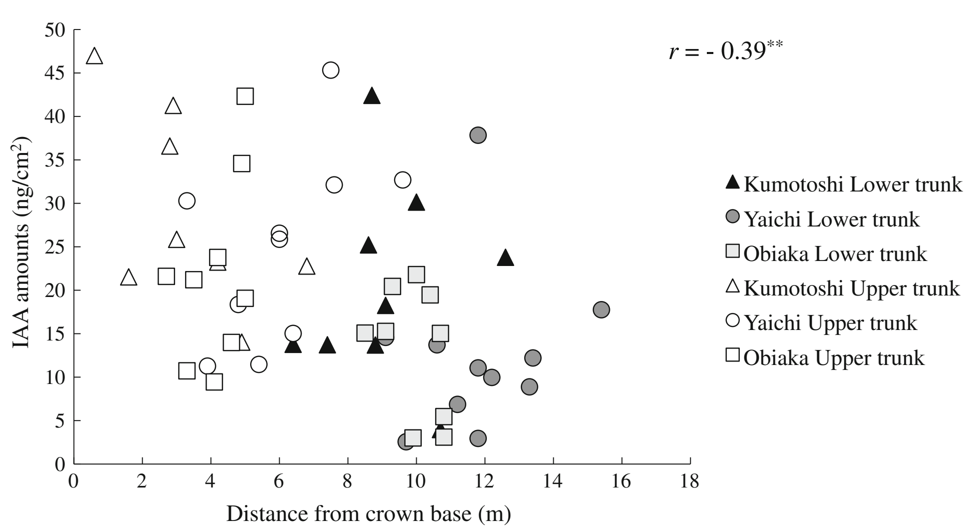

Table 2 Correlation coefficients between growth indexes and IAA amounts

Growth indexes	IAA amounts	
	Lower trunk	Upper trunk
CL	0.41 (0.026)*	0.36 (0.068)
CL ratio	0.40 (0.032)*	0.30 (0.124)
CW	0.27 (0.154)	0.12 (0.546)
CSA	0.38 (0.044)*	0.26 (0.184)
CV	0.36 (0.053)	0.23 (0.254)
H	0.19 (0.324)	0.26 (0.184)
DBH	0.25 (0.197)	0.28 (0.161)

The values represent the correlation coefficients between growth parameters and IAA amounts, and the values in parentheses represent the *p* values

DBH diameter at breast height, *H* tree height, *CL* crown length, *CW* crown width, *CSA* crown surface area, *CV* crown volume, *CL ratio* crown length-to-tree height ratio

* $p < 0.05$

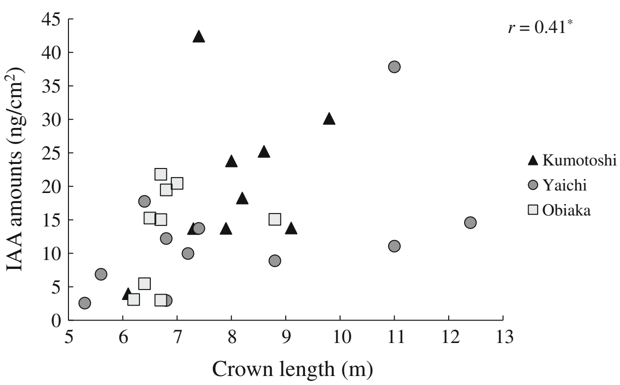

Fig. 5 Effect of crown length on IAA amounts at lower trunk of sugi cultivars. There was a significant positive correlation between the crown length and IAA amounts in sugi cultivars. *$p < 0.05$

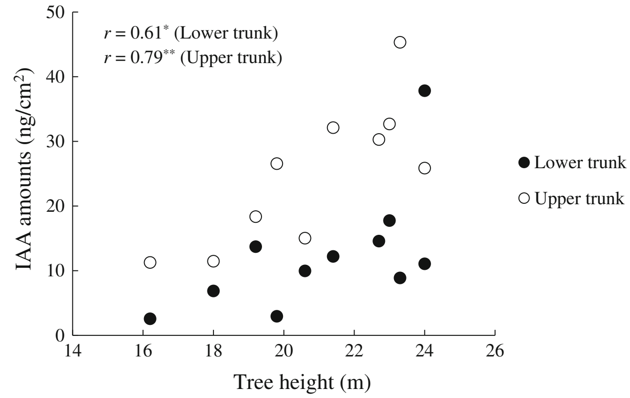

Fig. 6 Effects of tree height on IAA amounts in cambial region tissues of Yaichi. There were positive correlations between tree height and IAA amounts at the *lower* and *upper trunk*. *$p < 0.05$, **$p < 0.01$

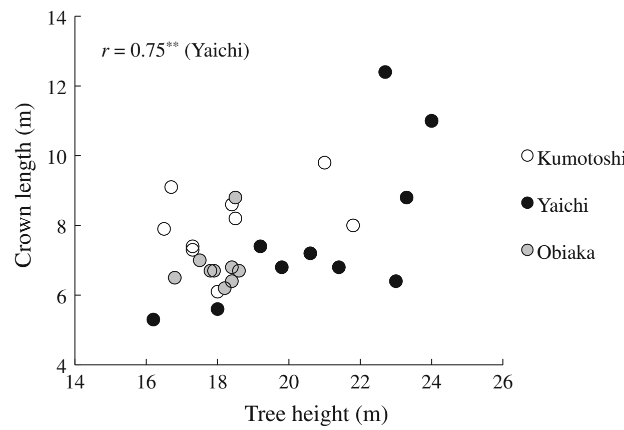

Fig. 7 Relationship between tree height and crown length in sugi cultivars. There was a significant positive correlation between tree height and crown length in Yaichi. **$p < 0.01$

cultivars (without pruning), it was statistically demonstrated that the distance from the crown and the crown length affected the variation of the IAA amounts in cambial region tissues in the trunk (Fig. 4, 5). These results of our study agree with the results of previous studies described above. From the results in Table 2, crown length was a growth index with a dominant effect on IAA amounts. As mentioned in introduction, elongating shoot and mature needles are believed to synthesize IAA and the synthesized IAA is transported to the trunk. Larger crown has larger number of elongating shoots and mature needles. In plantation trees, spaces for crown growth are restricted more severely in width direction than in longitudinal direction. Therefore, the variation of crown size in plantation trees may depend on the variation of crown length. The restricted crown growth in width direction may be the reason for the dominant effect of crown length on IAA amounts. The results obtained in this study are useful for future studies on the effects of IAA on xylem formation in sugi plantations. Especially, effects of the distance crown base and crown length on IAA amounts are useful for selection of sample trees and sampling positions. In trees of different age, it is assumed that tree height may be quite different with tree age. In these trees, CL ratio may be a more useful index on IAA amounts than crown length.

As described in the introduction, it was assumed that IAA was synthesized actively at elongating shoots [6–9]. Therefore, we hypothesized that Yaichi had greater IAA amounts at the lower and upper trunks because taller trees resulted from active shoot elongation. However, Yaichi trees did not have larger IAA amounts than other cultivars (Fig. 3). Yaichi trees with taller tree height had longer crown length (Fig. 7) and larger height of crown base. Based on the obtained results, these may have positive and

negative effects on IAA amounts. Kumotoshi had larger IAA amounts than other cultivars (Fig. 3). In this cultivar, distances from the crown base to sampling positions were smaller than other cultivars (Fig. 4). Therefore, it was assumed that the smaller distance from the crown base induced larger IAA amounts in Kumotoshi. Obiaka had smaller crown length than other cultivars. The characteristic in natural pruning may differ among cultivars. It was assumed that the characteristic in natural pruning affected crown length and height of crown base. Therefore, this characteristic may affect IAA amounts in the trunk of sugi trees. In sugi cultivars, the relationships between crown width and IAA amounts were not significant (Table 2). The shape of crown base observed from the ground in Kumotoshi and Obiaka was far from a circle, although that in Yaichi trees were close to a circle. Further study on more accurate non-destructive estimation of crown size of sugi cultivars (e.g., estimation using small footprint light detecting and ranging (LiDAR) raw data [20]) is needed. It was also reported that Kumotoshi had superior mechanical properties than other sugi cultivars [21, 22]. Mechanical properties are affected by anatomical wood properties (mainly by density and microfibril angle in secondary wall). In the future study, more precise study should be done on the effects of IAA amounts on these anatomical properties.

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